

Nocturnal resource defence in aphid-tending ants of northern Patagonia

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Abstract. 1. Interspecific competition plays a key role in the organisation of ant communities. In ant–plant interactions, individual host plants are usually occupied by a single ant colony, and co-occurring ant species compete for hosts. Here indirect evidence of competition between three dominant ant species that tend aphids on two biennial thistles in northern Patagonia is described, and a novel defensive behaviour in temperate ant assemblages is reported.

2. This study has found that: (i) dominant ant species were not spatially segregated, thus enhancing the probability of fights and invasions of host plants; (ii) ant species did not show preferences for a thistle species or for any plant characteristic, and thus all plants have similar chances of being colonised by all dominant ant species; (iii) the resident ant species remained on the same plant during the whole plant life cycle, monopolising plant resources (aphids); and (iv) all dominant species, whose nests are on the ground, assigned some ants to stay on the host plant during the night, when the low temperatures typical of this temperate environment greatly reduce foraging activities. When these ‘nocturnal guards’ were experimentally removed from the host plant, other ants from the same colony rapidly appeared showing aggressive behaviours.

3. Taking all these findings together, it is suggested that interspecific competition influences the distribution of ants on their host plants and involves nocturnal defensive behaviours despite unfavourable thermal conditions. This illustrates how habitat features, such as the short life cycle of thistles and the low night-time temperatures that reduce ant foraging and thus make plants more vulnerable to invasion, might affect the distribution and behaviour of ants.

Key words. Ant communities, aphids, competition, defensive behaviour, temperate regions, thistles.

Introduction

Interspecific competition plays a key role in the organisation of ant communities (Savolainen & Vepsäläinen, 1988; Andersen, 1992; Sanders & Gordon, 2003; Parr *et al.*, 2005). Several studies show that dominant ant species often limit the access of food resources to other, subordinate ant species, demonstrating

the occurrence of behavioural dominance hierarchies among ants (Adams, 1994; Human & Gordon, 1996; Andersen, 1997; Holway, 1999). Therefore, resource defence is crucial to prevent competitive exclusion in ant assemblages (Yamaguchi, 1995; Phillips & Willis, 2005). In ant–plant interactions, individual plants often host a single ant colony (Davidson *et al.*, 1989; Yu & Davidson, 1997) and, consequently, co-occurring ant species compete for host plants (Davidson & McKey, 1993; Clement *et al.*, 2008). Resident ants show different strategies to defend their host plant against other ant colonies (Heil *et al.*, 2001). For instance, ants can prune the surrounding vegetation to prevent competing ants from

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invading their colony (Janzen, 1969; Yumoto & Maruhashi, 1999; Federle *et al.*, 2002). Moreover, ant defensive tasks may vary spatially according to the risk of invasion (Gianoli *et al.*, 2008). Ant guards concentrate on the most vulnerable plant parts to impede the intrusion of other ant species (Heil & McKey, 2003). For example, the *Acacia* ant *Pseudomyrmex spinicola* has individuals specialised in a defensive function that aggregate at the base of the trunk, the only access point to their host plant, to repel ant invaders (Amador-Vargas, 2008).

Aphid-tending ants and their host plants in semi-arid temperate areas are a good system to study the spatial and temporal variation of ant defensive behaviours. First, overall, aphid honeydew is a key food resource for ants (Carroll & Janzen, 1973; Addicott, 1978); enhanced aphid abundance positively affects ant reproduction and colony expansion (Davidson, 1998; Yanoviak & Kaspari, 2000; Davidson *et al.*, 2003; Helms & Vinson, 2008). Consequently, ants strongly defend aphids against their natural enemies and other competing ants (Inouye & Taylor, 1979; Oliveira & Del-Claro, 2005; Phillips & Willis, 2005). Secondly, because most aphid-infested plant species in these ecosystems are short-lived (annual or biennial), aphid populations, and thus their tending ants, often need to relocate to other host plants. Thirdly, the typical cold nights of semi-arid temperate environments may offer a 'window of opportunity' to colonise occupied host plants for neighbouring ant colonies. In this type of habitat, ants often reduce their activity at night because of low temperatures (Cerdá *et al.*, 1998). If ant species within an assemblage vary in their cold tolerance, the most effective time to invade nearby plants may be during the night. This spatial and temporal dynamism (i.e. short-lived plants and cold nights with low ant activity) offers an ideal scenario to study changes in the defensive behaviour of ants.

In several areas of the Patagonian steppe, a semi-arid temperate environment, there is an aphid-mediated mutualism between ants and exotic thistles. In this association, two exotic thistle species, *Onopordum acanthium* and *Carduus thoermeri*, host four native ant species, *Brachymyrmex patagonica*, *Solenopsis richteri*, *Dorymyrmex tener* and *Dorymyrmex wolffuegeli* (Lescano & Farji-Brener, 2011). In contrast with co-occurring native plants, both thistle species are usually infested by aphids (Lescano & Farji-Brener, 2011). Several field observations suggest that thistles with aphids represent a valuable resource for which these ant species compete intensely: (i) aphid-infested thistles with no ant occupation are rare (Lescano & Farji-Brener, 2011); (ii) ant species rarely coexist on a single host plant (Lescano *et al.*, 2012); (iii) ants often show aggressive behaviour towards individuals from other ant species (M. N. Lescano, pers. obs.); and (iv) experiments facilitating the intrusion of neighbouring ants increase the probability that resident ones will abandon their host plant after a fight (M. N. Lescano, unpublished). Thus, the defence of thistles with aphids might be vital to prevent the loss of this valuable resource. In Patagonia, ant species are active only on warm days in the spring or summer, showing low or no activity during the typical cold nights (M. N. Lescano, pers. obs.). As discussed earlier, cold

nights may represent either a risk of being invaded or an opportunity to invade, depending on the cold tolerance of ant species.

In this field study in northern Patagonia, we carried out measurements to infer the occurrence of ant competition. In particular, we aimed at determining: (i) how the dominant ant species are distributed among thistles and through the seasons; and (ii) the activity of these ant species on their host plants during the day and during the night. Experimentally, we also attempted to exclude ants with nocturnal activity, in order to assess their effect on the risk of invasions by neighbouring ant species.

Material and methods

Study site and species

We carried out this study on the eastern border of the Nahuel Huapi National Park, located in Patagonia, Argentina (41°S, 72°W). This area comprises herbaceous /shrub steppe vegetation. The weather in the region is usually dry and cold, with an average precipitation of 600 mm and a mean annual temperature of 8 °C, but in summer, temperatures can range from −3 °C at night to 40 °C at midday (Farji-Brener & Tadey, 2012).

Field observations were performed in steppe areas along both sides of the road 237, because in these areas the study species (exotic thistles) are more abundant than in sectors distant from the road (Margutti *et al.*, 1996). The dominant vegetation in the study area is a mix of native species typical of Patagonian steppes, e.g. *Pappostipa speciosa*, *Mulinum spinosum*, *Imperata condensata*, *Plagiotyris tinctorius* and *Baccharis pingraea*, and exotic species such as *Bromus tectorum*, *O. acanthium*, *C. thoermeri* and *Verbascum thapsus* (Correa, 1969).

Carduus thoermeri (Nodding or Musk thistle) and *O. acanthium* (Scotch thistle) (Asteraceae: Cardueae) are among the most abundant exotic plants in the study area (Farji-Brener & Ghemandi, 2000, 2008). Both thistles are biennial, monocarpic herbs with high capacities for colonisation and dispersal, which confer on them the status of invasive species in several regions worldwide (Shea *et al.*, 2005). Seedlings of these thistle species emerge in spring and form a basal rosette that persists during its first year of life. In the following year, each rosette gives rise to one or several stems with numerous inflorescences. Plants die after flowering and there is no vegetative reproduction. The aphid *Brachycaudus cardui* (Aphididae: Macrosiphini) is a common herbivore of thistles and, because there are no native thistles in the study area, is the most frequent aphid species on both exotic thistle species (Lescano & Farji-Brener, 2011). The aphid colonies are located beneath leaves, on stems and at the inflorescence bases. Four native ant species usually tend *B. cardui*: *Dorymyrmex tener*, *D. wolffuegeli* (Dolichoderinae), *B. patagonica* (Formicinae) and *S. richteri* (Myrmicinae). These species are rarely found sharing a host plant, and, when they do, *D. wolffuegeli* is usually the subordinate one (Lescano *et al.*, 2012). Thus,

for this work we focused on *B. patagonica*, *D. tener*, and *S. richteri* as dominant species. All of these ant species nest in soil, under stones or leaf litter, but never on thistles (M. N. Lescano and A. G. Farji-Brener, pers. obs.).

Spatial segregation of ant species

To test whether the dominant ant species select different habitat patches (i.e. whether they are spatially segregated), we walked along an area of 100×1000 m to locate neighbouring thistles occupied by different tending ant species. We counted the number of neighbours that met this condition. Additionally, we placed pitfall traps around 41 thistles present in the area (six pitfalls per thistle) to collect tending ants at ground level. Sampled thistles were ~ 20 m apart. Pitfalls were plastic cups (10 cm diameter and 10 cm depth) that were 80% filled with a preserving solution (propylene glycol 40%) and buried at ground level. All pitfalls were opened for 7 days and checked at the end. To determine the ant species present around each thistle, we pooled the six pitfalls per plant in a single sample ($n = 41$).

Ant preference for thistles and residence time

In order to evaluate whether ant species prefer as host one of the two thistle species or particular characteristics of individual thistles, we measured 49 plants (23 plants of *C. thoermeri* and 26 plants of *O. acanthium*) occupied by a single ant species (or with *D. wolffuegeli* as the subordinate species). In each focal plant, we counted the total number of leaves and inflorescences per plant, measured the plant height, estimated the mean aphid density (aphids cm^{-2}), and determined the tending ant species present. The estimation of aphid density was based on counts made in digital photographs of different subgroups of each population (which we named 'food groups') chosen at random on each focal plant. We considered as a 'food group' a spatially discrete set of individuals occupying a leaf, stem or inflorescence. We took 10 digital photographs of different food groups per plant and we then averaged the values of each photo to get an estimation of aphid density per plant (see Lescano *et al.*, 2012 for details). Because the presence of ant species did not differ significantly between thistle species (see the Results section), we compared characteristics of thistles regardless of their identity (Kruskal–Wallis test; sample size obtained by random sampling: *B. patagonica*, 24 thistles; *D. tener*, 18 thistles; *S. richteri*, seven thistles). To examine whether the same ant species stayed on the same host once it was colonised, 43 thistles were visited two to three times during the summer (visits took place after 15, 45 and 60 days). In the same season, nine plants at rosette stage were visited and these plants also were visited the following year (adult stage). On each visit, we documented the identity of the resident tending ant.

Activity of ant species during the day and night

To determine the activity of each tending ant species at different times, we visited 72 thistles at different periods during the day (08.00–10.00 hours, 10.01–12.00 hours, 12.01–14.00 hours, 14.01–16.00 hours, 16.01–18.00 hours, and 18.01–20.00 hours) and we counted the number of ants min^{-1} five consecutive times on different plant parts. These visits were split on different days of summer and not all individuals were visited in all time periods. The activity of each ant species per plant was estimated as the sum of the number of ants counted per minute (for a total of 5 min). We calculated the mean ant activity during each time period from the three ant species.

To observe nocturnal ant activity on host thistles and describe their behaviour, on different days we visited 31 thistles with different ant species as resident between 02.00 and 07.00 hours. To test whether these nocturnal ants prevent the presence of intruders on their host plant, we counted the number of ants min^{-1} and then we removed all individuals present in a subsample of 10 focal thistles (four, three and three thistles with *S. richteri*, *D. tener* and *B. patagonica* as resident species, respectively) using an insect aspirator. After the exclusion of individuals from their host plants, we documented the appearance of other individuals or other ant species on the plant. Additionally, on five thistles we attached HOBO H8 data loggers (Onset Computer Corporation, Bourne, MA, USA) to record the temperature in each plant every 1 h over a week.

Results

Spatial segregation of ant species

The home ranges of the dominant ant species overlap. Foragers of *B. patagonica*, *D. tener* and *S. richteri* were usually found in the same habitat (i.e. occupying neighbouring plants) and were captured in the same pitfall several times. Thus, we found 80 pairs of neighbouring thistles with different resident tending ants, with distances between them of only ~ 1 m. Moreover, in 63% of the pitfalls, we found two of the three ant species, and in 20% of the pitfalls we found the three tending ant species. Furthermore, when the three ant species were collected in the same traps, there was no clear dominance hierarchy, as the resident ant species on the nearest plant (around which we placed pitfall traps) was not always the same. The nearest thistle was occupied three times by *B. patagonica*, three times by *S. richteri* and twice by *D. tener*, regardless of their relative abundance in traps. Although the three ant species did not show spatial segregation, they were rarely observed coexisting on the same host plant.

Ant preference for thistles and residence time

All ant species were found on both thistle species in similar proportions, showing no preference ($\chi^2 = 1.49$, d.f. = 2,

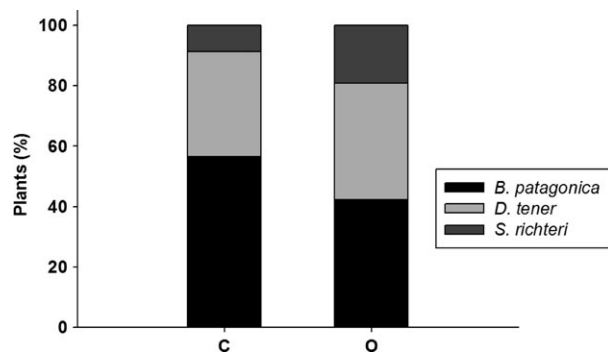


Fig. 1. Percentage of plants with different resident aphid-tending ant species. C: *Carduus thoermeri* and O: *Onopordum acanthium*.

Table 1. Thistle traits (mean \pm SE) with different resident ant species. Differences between ant species were tested by Kruskal–Wallis test.

Thistle traits	Ant species			P
	<i>Brachymyrmex patagonica</i>	<i>Dorymyrmex tener</i>	<i>Solenopsis richteri</i>	
No. of leaves	53.87 \pm 6.14	57.88 \pm 6.08	63.71 \pm 16.35	0.59
No. of inflorescences	14.55 \pm 0.65	13.61 \pm 0.77	18.42 \pm 2.4	0.96
Height (m)	1.16 \pm 0.06	1.19 \pm 0.05	1.04 \pm 0.06	0.66
Aphids cm ⁻²	10.35 \pm 2.03	13.63 \pm 1.69	7.16 \pm 2.26	0.07

$P = 0.47$; Fig. 1). Furthermore, the different ant species colonised plants with similar characteristics (Table 1). Once a thistle was occupied, the resident ant species remained on the same plant throughout the day and the year. Moreover, all the plants that were observed along their entire life cycle (2 years) were always occupied by the same ant species.

Activity of ant species during the day and night

During daytime hours, the three ant species actively tended aphids but differed in the number of workers ($H = 19.35$, d.f. = 2, $P < 0.001$). *Brachymyrmex patagonica* and *D. tener* showed higher activity (81 ± 9 and 75 ± 9 ants per 5 min, mean \pm SE, respectively), whereas *S. richteri* showed less activity (24 ± 4 ants per 5 min, mean \pm SE). The activity of the three ant species fluctuated throughout the daytime observation period (Fig. 2), during which ants were always observed moving along the plant and tending aphids, and were never observed motionless at the base of plants or leaves. At night, the activity of the three ant species sharply decreased (Fig. 3), but ants never completely abandoned their host plant. The numbers of workers on a plant during the night were similar among the three species, but represented different colony effort regarding the number of active ants of each species. Thus, *B. patagonica* and *D. tener* allocated, on average, 13% and 9% of individuals assigned to tend aphids during the daytime,

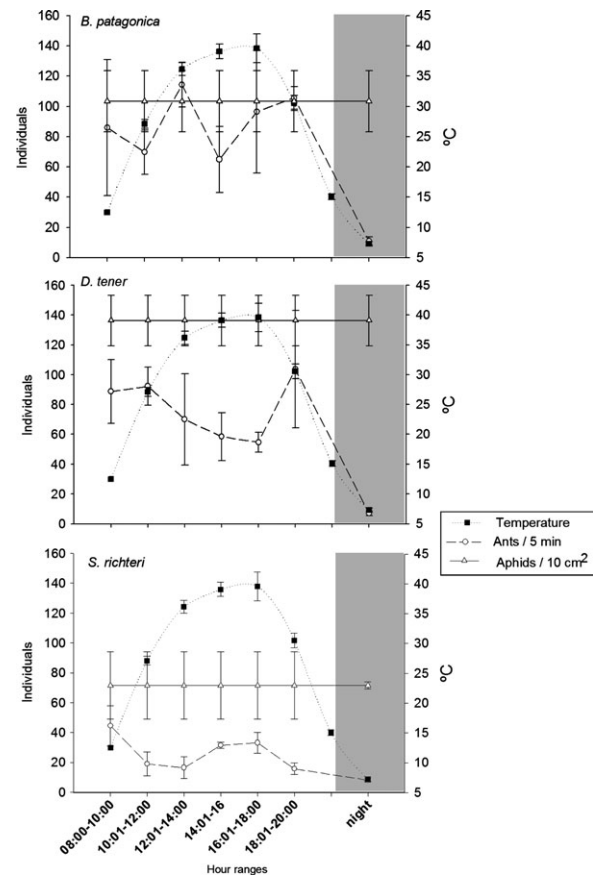


Fig. 2. Number (mean \pm SE) of ants (ants per 5 min) and aphids (aphids per 10 cm²), and temperature (°C) throughout the day and at night (from 02.00 to 07.00 hours): (a) *Brachymyrmex patagonica*; (b) *Dorymyrmex tener*; (c) *Solenopsis richteri*.

respectively. However, the ant species with less activity during the day, *S. richteri*, assigned 34% of their day workers to do night tasks. Individuals that remained on their host at night were always motionless at the base of the trunk and beneath the plant leaves, and were never observed tending aphids. Observations took place at different times during the night to detect possible changes in the activity of ants, but this scenario did not change, except when we altered the host plant to experimentally remove nocturnal ants. Immediately after we excluded ants from their host plants, other individuals from the same colony appeared at the base of the thistle and patrolled the plant. For this reason, we could not carry out the experiment to exclude nocturnal ants as a means of promoting invasion by nearby ant colonies.

Discussion

Four indirect lines of evidence suggest that interspecific competition plays an ecological role structuring the assemblage of aphid-tending ants in northern Patagonia. First, dominant ant species were not spatially segregated, thus enhancing the probability of invasions between neighbouring host plants.

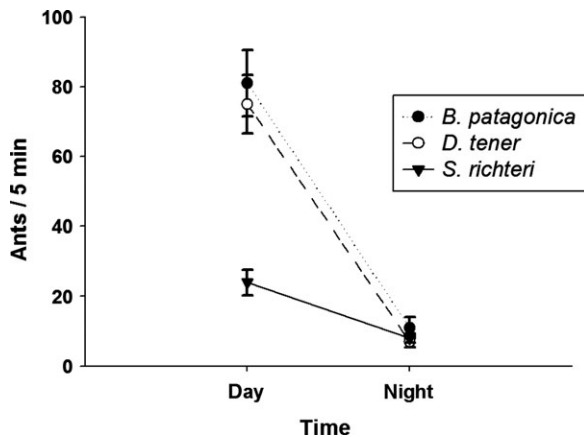


Fig. 3. Mean ant activity (ants per 5 min) during the day (from 08.00–20.00 hours) and night (02.00–07.00 hours).

Secondly, dominant ant species did not show preferences for different thistle species or for particular plant characteristics; thus, they were not segregated at the plant level. Thirdly, the resident ant species often remained on the same plant during the whole plant life cycle, monopolising plant resources. Finally, all dominant species assigned ants to stay on their host plant during the night, when low temperatures greatly reduce their activity, despite the fact that their nests were on the ground and that aphids are not tended at night. Moreover, when these 'nocturnal guards' were removed, other ants from the same colony, which were sheltered on the host plant, rapidly appeared showing aggressive behaviours. Taking all these findings together, we suggest that interspecific competition influences the distribution and behaviour of these ant species.

When competing ant species do not have exclusive foraging territories, they are frequently involved in aggressive interactions. Accordingly, many ant species are spatially segregated as an economic strategy to secure food resources (Levings & Traniello, 1981; Hölldobler & Wilson, 1990). For example, the establishment of mutually exclusive foraging areas by dominant ant species in tropical habitats diminishes the energy allocated to preserve their resources (Jackson, 1984). However, depending on the spatial and temporal variation of food availability, the segregation at patch level could be disadvantageous. Ants usually show territoriality when food resources are relatively stable in space and/or in time (Blüthgen & Stork, 2007). For example, in plant communities dominated by long-lived trees and shrubs, ant species often have mutually exclusive distributions, forming a 'mosaic' of territories (Jackson, 1984; Adams, 1994). Here we found that the dominant ant species of this assemblage co-occur in the same patch and colonise host plants with similar characteristics, suggesting the absence of territorial segregation. Contrary to the example described earlier, in this system resources are temporally and spatially dynamic, thus discouraging the formation of fixed territories. First, ant colonies live more years than their host plants (thistles are biennials), forcing ants to colonise new aphid-infested thistles several times during the colony life cycle. Secondly, the phenology of thistles is not perfectly synchronised, so that not

all individuals are in the same phenological stage or infested with aphids at the same time or in the same patch. Finally, aphid colonies respond to these phenological and demographic changes, moving between plants that offer the best shelter and food.

Since all three ant species share the territory, an alternative way to reduce their conflict could be the differential selection of resources based on its quantity and/or quality, thus showing dominance hierarchies (Blüthgen & Fiedler, 2004). For example, two species of the genus *Pseudomyrmex* that feed and nest on *Acacia cornigera* coexist in a tropical deciduous forest in Mexico; but *Pseudomyrmex ferrugineus* colonises larger plants than *Pseudomyrmex gracilis* (Sánchez & Rico-Gray, 2011). In the Patagonian steppe, no ant species showed a preference for thistles with differential aphid density or plants that differ in height and number of leaves and inflorescences. Consequently, ant species do not segregate at plant level, enhancing the probability of aggressive interspecific interactions on the same aphid-infested thistle. In summary, the low temporal and spatial predictability of resources may stimulate competitive behaviours at the individual host plant level.

Other ant community studies, in which preferences and monopolisation by the dominant ants have not been reported, showed that coexistence among species that use the same resource is facilitated by their different abilities to forage in a variable abiotic environment (Levins *et al.*, 1973; Bestelmeyer, 2000). Accordingly, different seasonal or diurnal activity patterns could avoid competition between ant species (e.g. Cerdá *et al.*, 1997, 1998; Bestelmeyer, 2000). In the system studied here, ant activity is restricted to the warm seasons (spring–summer) due to the marked seasonality at this latitude; and even during the warm seasons the low night temperature limits ant activity to daytime periods. This could promote a daily turnover of ant species on a thistle with aphids. Thus, every morning, a contest for resources to monopolise (an aphid-infested thistle) could take place. Accordingly, during the night we observed in the three dominant ant species the presence of immobile workers at the base, under the basal leaves or on other leaves. We think that these ant individuals function as nocturnal guards, preventing invasion of their host plant. These guards are not feeding, as aphids are never tended at night (M. N. Lescano, pers. obs.). Neither are they nesting, because all tending ant species nest on the ground. And they are not resting, as they are highly alert and easily disturbed. When their host plant is disturbed, formerly motionless workers mobilise quickly and recruit more individuals. Finally, when these ants are experimentally removed, other ants of the same colony appear from different parts of the host plant showing aggressive behaviours. All of this strongly suggests that the motionless ants present on the thistles at night play a defensive function.

The high efficiency of ant-guards at preventing the access of potential invaders has been mainly documented in neotropical ant–acacia systems (Heil & McKey, 2003; Amador-Vargas, 2008). Unlike the pattern observed here, in tropical systems a substantial number of workers actively patrol their host throughout the day and night (Raine *et al.*, 2004). To our

knowledge, this is the first record of nocturnal defensive behaviour in ants associated with plants in temperate systems. The lack of activity of the three ant species at night suggests that all species have similar cold tolerance. Moreover, the assignment of workers to protect the host plant at night might be costly; ants can suffer morphological or physiological injuries after long-term exposure to very low temperatures (Maysov & Kipyatkov, 2011). Accordingly, all dominant species assign a similar (and low) number of ants to this nocturnal function (~10 ants per plant, see Figs 1 and 3). However, this may represent a different colony effort regarding the number of active ants of each species. While for the ant species with more active ants and more thistles colonised (*B. patagonia* and *D. tener*) nocturnal guards represent only ~10% of their workers active diurnally, *S. richteri* – the species with less active workers and a low number of colonised thistles – assigns 34% of active workers diurnally. This could represent further indirect evidence of the importance of nocturnal guards, because the most vulnerable ant species (the one with less active ants and fewer thistles colonised) assigns several times more workers (relatively) than the other dominant ant species. Further observational and more experimental evidence is needed, however, to support the hypotheses that interspecific competition drives ant distribution among thistles with aphids and that nocturnal ant guards play a key role in the system. Nevertheless, the evidence obtained in this study is the first step in understanding how competition operates in this ecological scenario, which is highly dynamic at both the spatial and temporal scales and is also thermally constrained. The study also illustrates how these conditions may select a particular defensive behaviour: the presence of nocturnal guards during cold nights.

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